THE SALAMANDER *BRACHYCORMUS NOACHICUS* FROM THE OLIGOCENE OF EUROPE, AND THE ROLE OF NEOTENY IN THE EVOLUTION OF SALAMANDERS

by ZBYNĔK ROČEK

ABSTRACT. All available material of the late Oligocene salamandrid amphibian *Brachycormus noachicus* is redescribed, with a reconstruction of its skeleton and an evaluation of its range of variation. This neotenous salamandrid is strikingly similar, in the shape of its visceral skeleton, to larvae of the contemporary *Triturus* in the final stages of metamorphosis, and to neotenous specimens of *Triturus alpestris*. However, in contrast to the latter facultative neotenous larvae, *Brachycormus*, though morphologically underdeveloped, was fully ossified. Occurrence of neoteny in the Tertiary tailed amphibians was associated with the global deterioration of climate during the Oligocene (a significant drop of mean annual temperatures and a broader range of annual temperatures). Prolongation of cold meant that larvae were not able to metamorphose in time and thus became permanent water dwellers. Subsequent improvement of climate in the Miocene permitted the amphibious life-cycle to resume; this was accompanied by completion of metamorphosis of the visceral skeleton but retarded osteogenesis in other respects (e.g. incomplete frontotemporal arch). Thus, *Brachycormus* may be taken as a phylogenetic link between the Oligocene Caudata related to *Chelotriton* and the contemporary genus *Triturus*.

THE first reported Tertiary tailed amphibians (apart from *Andrias scheuchzeri*, known since 1726, and initially variously misinterpreted as a diluvial human, catfish and reptile) were described by Goldfuss (1831) from the region of Siebengebirge near Bonn, Germany, namely from Orsberg near Erpel, Stösschen near Linz, and Rott near Hennef, where the famous 'Blatterkohle' underground mines operated until the 1870s. Biostratigraphy, based on the mammalian fauna found at Rott, suggests an uppermost Oligocene age for all these localities (von Koenigswald *et al*. 1992, p. 313) and the deposits represent a lacustrine biotope. Although the specimens are sometimes near complete articulated skeletons, the bones were dissolved and only natural moulds survive. In most specimens, dorso-ventral compression has resulted in the crushing of three-dimensional bones and structures such as vertebral centra and girdles, the twisting of ribs along their longitudinal axes, and of the tail through 90° relative to the trunk, because of its antero-posteriorly expanded haemal and neural vertebral processes, thus preserving its lateral aspect along the horizontal plane of the matrix. Only the long, thin bones of the limbs are preserved as relatively good imprints.

Goldfuss undoubtedly used for comparison the newts and salamanders that occur in the region today, namely *Triturus* and *Salamandra*. This may be concluded not only from the names he gave to his fossils (*Salamandra ogygia*, *Triton noachicus*) but also from his illustrations. The osteological details that he illustrated are not always observable on the specimens. The skeletons are incomplete in some cases (e.g. the left hind leg and the tail are missing in the holotype of *Brachycormus noachicus*; see Text-fig. 1), but Goldfuss illustrated them (1831, pl. 13, figs 5–6) as if they were complete. It can only be guessed as to whether the specimens were originally complete and damaged later, or if the illustrations are idealized reconstructions by Goldfuss (see also the note by von Meyer 1860, p. 64, who wrote as early as 30 years after Goldfuss's publication, that the holotype was 'in such bad shape that precise illustration of the complete animal is no longer possible').

In subsequent decades, further specimens were found at the same localities, and these were described by von Meyer (1852a, 1852b, 1858, 1860, 1863). Von Meyer (1860) based his redescription of *Brachycormus noachicus* on five specimens (including the original specimen of Goldfuss), and all

but two are in the Paläontologisches Institut der Universität Bonn, and not lost as Estes (1981, p. 71) believed. The exceptions are one specimen that was preserved in lateral aspect (see von Meyer 1860, pl. 7, fig. 8) which does appear to be lost, and another which was sold to the British Museum (Natural History) where it is deposited as BMNH 30268. Von Meyer also recognized correctly the difference between these fossils and the genus *Triturus* and proposed (von Meyer 1860, p. 71) a new generic name *Brachycormus*.

After von Meyer's work, this material was not restudied until 1981 when Estes published his review of the fossil Caudata. He obviously did not investigate the original material from Rott thoroughly, but placed some of Herre's (1949) taxa, namely *Oligosemia gerhardti* and *Tylototriton kosswigi*, into the synonymy of *Brachycormus noachicus*.

Already Goldfuss (1831, p. 127) had pointed out that this amphibian differs from contemporary *Triturus* in its simplified skull structure. Von Meyer (1860, pl. 67) recognized some larval characters in its structure and Estes (1981, p. 71) stated that '…some of the individuals were gilled larvae, although their otherwise adult morphology indicates that they were near metamorphosis'. Neoteny and paedomorphosis are generally considered important phenomena in vertebrate evolution (Gould 1977) and, because the early phylogenetic origins of both Anura and Urodela are undoubtedly associated with developmental abbreviation (see temnospondyls described by Bolt 1969, 1977, 1979; Warren and Hutchinson 1988, 1990; Warren and Schroeder 1995), it became obvious that neoteny and paedomorphosis played an important role also in urodelan origin and evolution (Milner 1988, p. 94) and that their occurrence in fossil forms deserves some attention. Study of neoteny also has a practical impact on caudate systematics, because superficially different forms may actually be closely related if comparison is based on different developmental stages of the taxa under investigation. Therefore, the recognition of larval characters in the structure of fossil amphibians is important, as well as an understanding of those factors that influence (and modify) normal development. This, together with clarification of the phylogenetic position of the genus *Brachycormus*, is the aim of the present paper.

Institutional abbreviations are as follows: BMNH, The Natural History Museum, London; MB, Museum für Naturkunde, Berlin; NMP, National Museum, Prague; PIUB, Paläontologisches Institut der Universität, Bonn; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

SYSTEMATIC PALAEONTOLOGY

Order CAUDATA Scopoli, 1777
Family SALAMANDRIDAE Gray, 1825

Genus BRACHYCORMUS von Meyer, 1860

Diagnosis. As for *Brachycormus noachicus*, the type and only species.
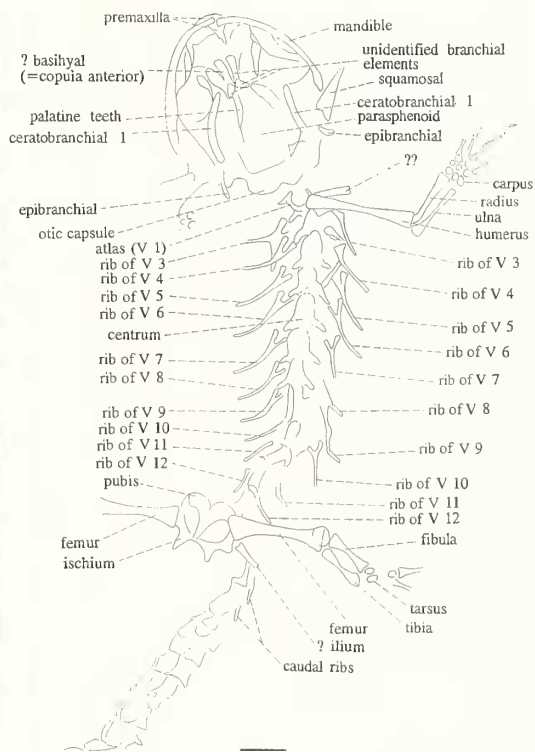
Brachycormus noachicus (Goldfuss, 1831)

Text-figures 1–6, 8.

1831   *Triton noachicus* Goldfuss, p. 126, pl. 13, figs 6–7.
1831   *Triton Noachicus*; Goldfuss, p. 230.
1852   *Triton Noachicus*; Dechen, p. 502.
1860   *Brachycormus noachicus* (Goldfuss); von Meyer, p. 67.
1863   *Triton (Brachycormus) noachicus* Goldfuss; von Meyer, p. 297.
1890   *Molge noachica* (Goldfuss); Lydekker, p. 136.
1935   *Triturus noachicus* (Goldfuss); Herre, p. 54.

| 1949 | *Oligosemia gerhardti* Herre, p. 229. |
1949	*Oligosemia ankeli* Herre, p. 229.
1949	*Tylototriton kosswigi* Herre, p. 230.
1955	*Tylototiton kosswigi* (ex err.); Herre, p. 799.
1981	*Brachycormus noachius* (ex err.); Estes, p. 71.

A complete synonymy up to 1990 is given in von Koenigswald *et al.* (1992, p. 319).

Holotype. PIUB Ro 4429 (previously 13207A), a mould of an almost complete skeleton in ventral aspect (Text-fig. 1).
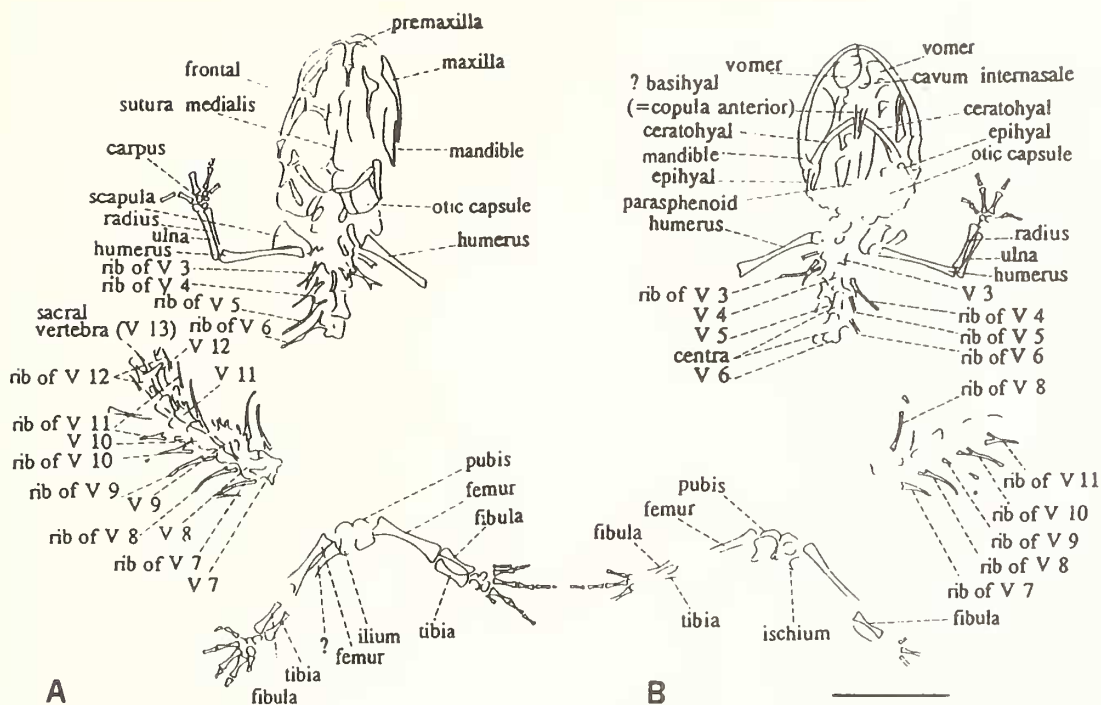

TEXT-FIG. 1. *Brachycormus noachicus* (Goldfuss, 1831). PIUB Ro 4429, holotype; (formerly Goldfuss 1307 A); Upper Oligocene; Orsberg. Scale bar represents 2 mm.

Comment. The original specimen figured by Goldfuss (1831, pl. 13, figs 6–7) was designated as the neotype by Estes (1981, p. 71). Curiously enough, Estes stated that the specimen was no longer in the collection of the Paläontologisches Institut der Universität Bonn and was probably lost. This statement was repeated by von Koenigswald *et al.* (1992, p. 320) who believed that the neotype was BMNH 30268 illustrated by Estes (1981, fig. 20a). However, the holotype was found, under the catalogue number 1307, in the collection of Goldfuss's types and Estes obviously saw it because there is a note written by his hand in the box with the specimen, namely '1307A = Typusexamplar (= Neotype by subsequent designation: Richard Estes 1979 ms, Handbuch der Paläoherpetologie)' and he even stated (loc. cit.) that it is well preserved. Now the specimen has a new collection number, PIUB Ro 4429, and it should be emphasized that it is not a neotype but the holotype by implication, and Estes's designation of the neotype is invalid. A second specimen PIUB Ro 4053a + b,
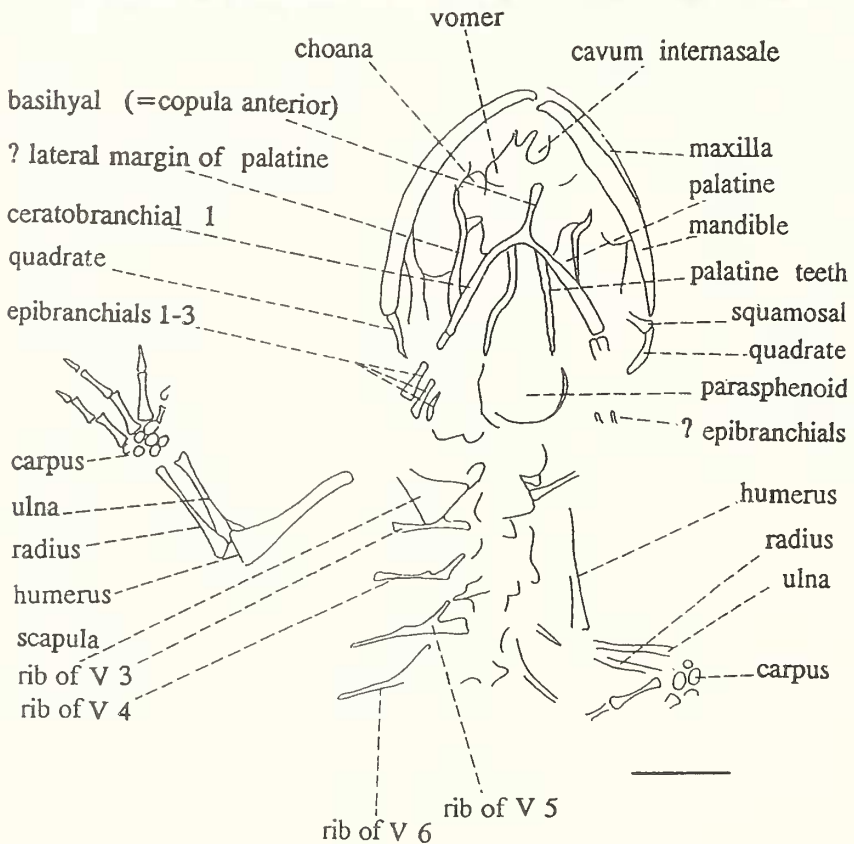
TEXT-FIG. 2. *Brachycormus noachicus* (Goldfuss, 1831). PIUB Ro 4244*b*; Upper Oligocene; Orsberg. Skull and anterior part of postcranial skeleton in ventral view. Scale bar represents 2 mm.

TEXT-FIG. 3. *Brachycormus noachicus* (Goldfuss, 1831). Upper Oligocene; Orsberg. PIUB Ro 4245*a–b*. A, skeleton in dorsal view and B, in ventral view. Scale bar represents 5 mm.
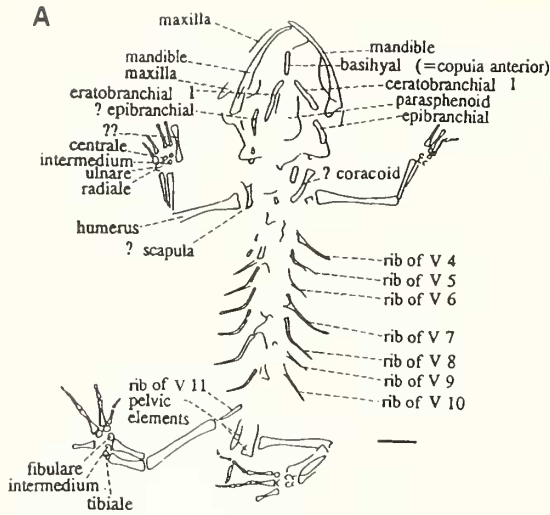
originally described by von Meyer (1860, pl. 8, fig. 7) was designated as the paratype (Koenigswald *et al.* 1992, p. 320) but this designation is also invalid, according to the International Code of Zoological Nomenclature.

Horizon and locality. Upper Oligocene; Orsberg near Erpel, Germany.
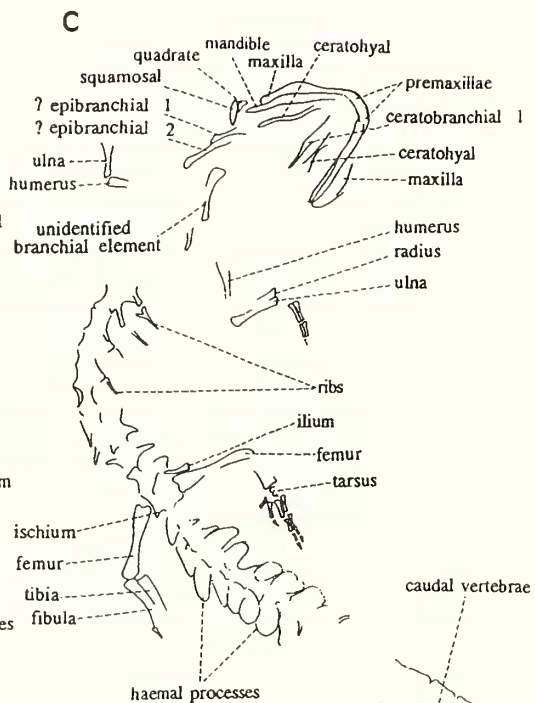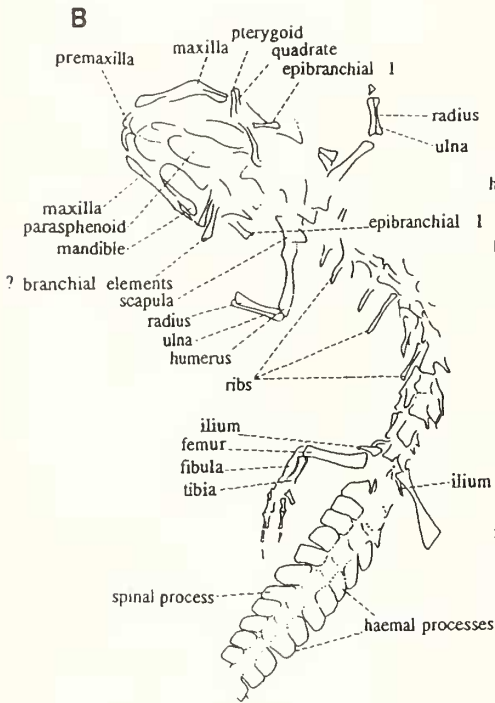
Referred material. All from the Upper Oligocene of the Siebengebirge Region near Bonn, Germany. From the type locality: PIUB Ro 4244*a*, *Ro* 4244*b* (Text-fig. 2), Ro 4245 (Text-fig. 3) and Ro 4430 (previously Goldfuss 1307B) (Text-fig. 4A). Attributed to Orsberg but locality uncertain: MB Am.928.1–2 (holotype of *Oligosemia gerhardti* Herre, 1949) (Text-fig. 6A), MB Am.930.1 (holotype of *Tylototriton kosswigi* Herre, 1949) (Text-fig. 6B). From Stösschen near Linz: PIUB Ro 4053 (Text-fig. 4B–C). From 'Rott' (exact locality uncertain): BMNH 30268 (Text-fig. 5).

Diagnosis. Brachycormus is closely related to *Triturus* but differs from it in that (1) it is neotenous, with an ossified hyobranchial skeleton, specifically the copula anterior, ceratobranchial 1, ceratohyal and epibranchials, and with external gills apparently present, and (2) the skeleton shows incomplete ontogenetic development, with frontotemporal arch absent and vomers probably not fused with palatines, although it reached the final stage of ossification (including elements such as the carpals and tarsals).

Description. All specimens from Orsberg and Stösschen are preserved as natural moulds in matrix. It is obvious that in those specimens in which both counterparts are available, the whole skeleton was compressed dorsoventrally so that in the counterpart, which displays the dorsal aspect, ventral elements are also visible, though to a lesser degree. Nevertheless, the topographical relations between elements such as the maxilla and mandible may be deduced from these specimens (e.g. Text-figs 3A, 4B–C).

A

maxilla
mandible
maxilla
mandible
basihyal (=copula anterior)
ceratobranchial 1
eratobranchial 1
? epibranchial
parasphenoid
epibranchial
??
centrale
intermedium
ulnare
radiale
? coracoid
humerus
? scapula
rib of V 4
rib of V 5
rib of V 6
rib of V 7
rib of V 8
rib of V 9
rib of V 10
rib of V 11
pelvic
elements
fibulare
intermedium
tibiale

TEXT-FIG. 4. *Brachycormus noachicus* (Goldfuss, 1831). A, PIUB Ro 4430 (formerly Goldfuss 1307B); Upper Oligocene; Orsberg. Skeleton in ventral view. B–C, PIUB Ro 4053*a*–*b*; Upper Oligocene; Stösschen. Skeleton in B, dorsal view and C, ventral view. Scale bar represents 2 mm.

B

premaxilla
maxilla
pterygoid
quadrate
epibranchial 1
radius
ulna
maxilla
parasphenoid
mandible
epibranchial 1
? branchial elements
scapula
radius
ulna
humerus
ribs
ilium
femur
fibula
tibia
ilium
spinal process
haemal processes

C

squamosal
quadrate
mandible
maxilla
ceratohyal
? epibranchial 1
? epibranchial 2
premaxiliae
ceratobranchial 1
ulna
humerus
ceratohyal
maxilla
unidentified
branchial element
humerus
radius
ulna
ribs
ilium
femur
tarsus
ischium
femur
tibia
fibula
caudal vertebrae
haemal processes

The snout–vent length is about 23 mm. The skull is longer than broad (LC:LtC 1·13–1·30) in the PIUB specimens; however, the two MB specimens collected by Bergemann (Text-fig. 6A–B) have skulls which are slightly broader than long (see Table 1). Although Herre (1949, p. 227) attributed these two specimens to the Orsberg locality, from which most of the others came, there are some doubts as to the accuracy of this attribution, because the locality is not given on the specimen labels and it is obvious that the specimens were

TEXT-FIG. 5. *Brachycormus noachicus* (Goldfuss, 1831). BMNH 30268. Skeleton in dorsal view. Arrows mark positions of caudal vertebrae. Scale bar represents 5 mm.
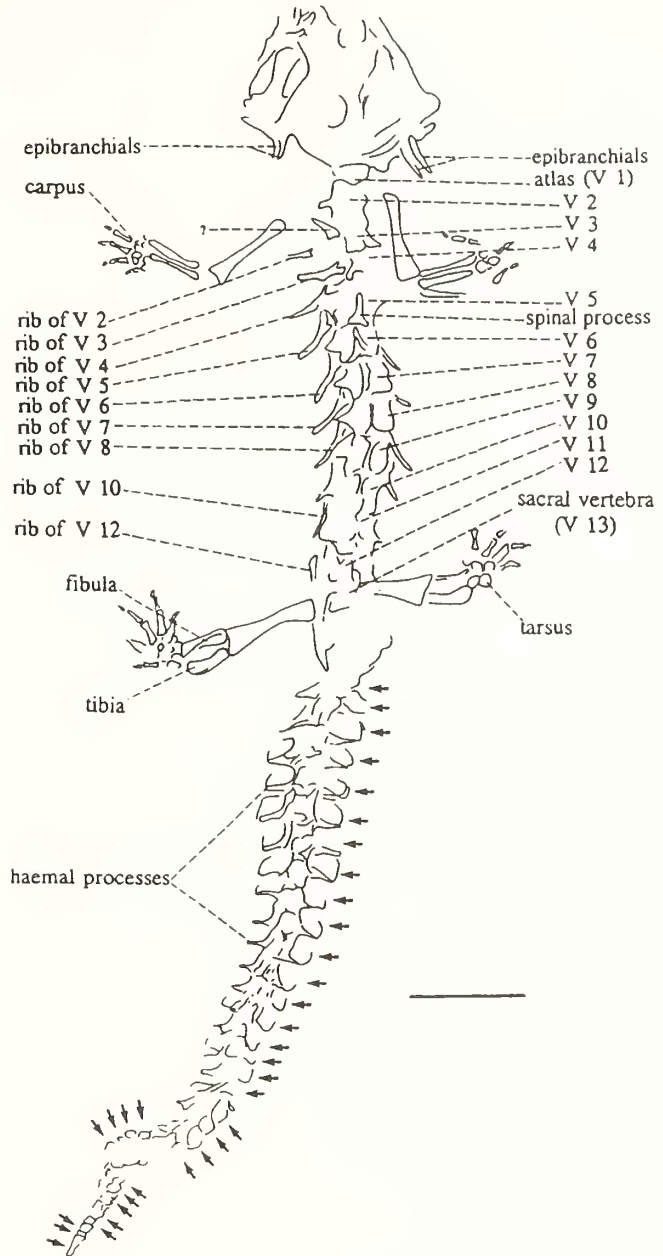
collected in the first decades of this century long after underground mining had ceased (*c.* 1860). Later collectors searched for fossils in spoil heaps on the surface and sometimes assigned these specimens to the locality of the original site where most specimens had previously been collected (likewise for BMNH 30268 for which the locality is recorded as 'Rott' although the nature of matrix indicates either Orsberg or Stösschen).

The premaxillae (and presumably also the other jaw elements) are dentate. As suggested by symmetrical position of premaxillae in PIUB Ro 4245*a* which represents the skeleton in dorsal view (Text-fig. 3A) and PIUB Ro 4053*b* (Text-fig. 4C), they were fused. The frontal processes of the premaxillae were long and slender, and
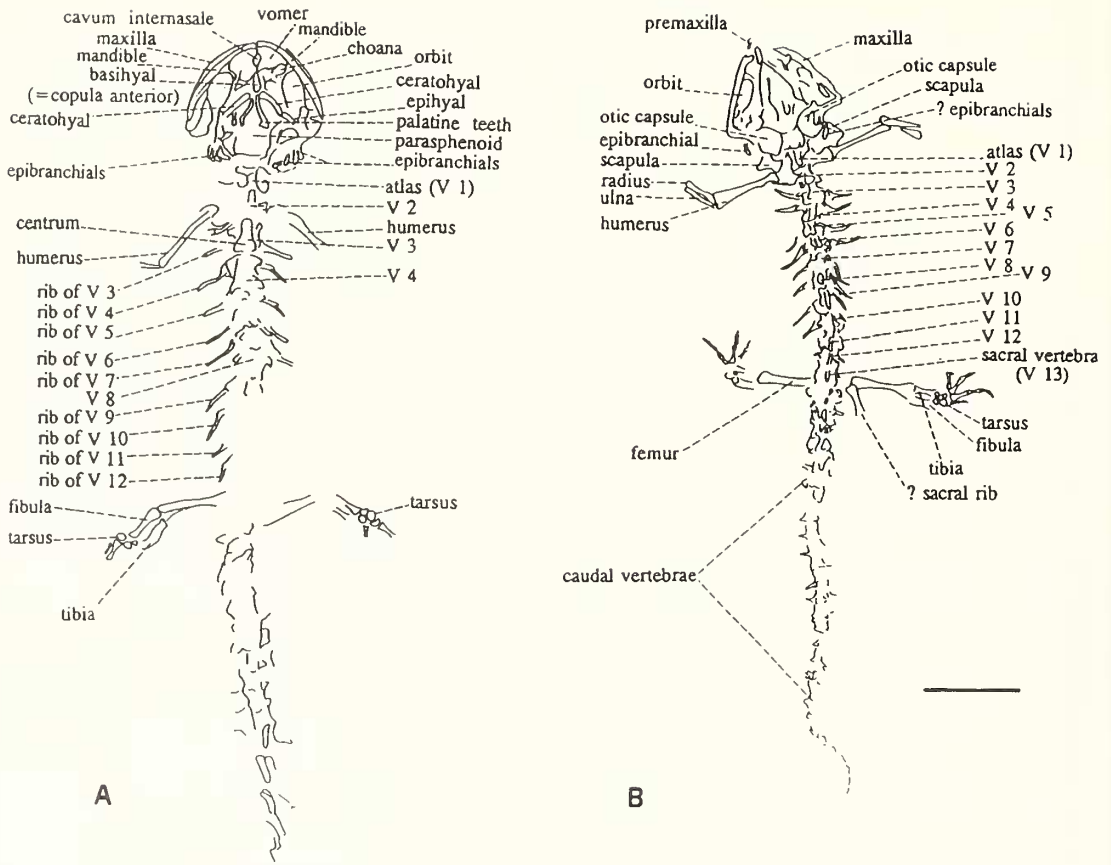
TEXT-FIG. 6. *Brachycormus noachicus* (Goldfuss, 1831), A, MB Am.928.1–2, holotype of *Oligosemia gerhardti* Herre, 1949; skeleton in ventral view. B, MB Am.930.1, holotype of *Tylototriton kosswigi* Herre, 1949; skeleton in dorsal view. Scale bar represents 5 mm.

probably fused to a variable extent. In palatal view, the lamina horizontalis of each premaxilla is in contact with the vomer and with the lamina horizontalis of the maxilla. The vomers are separated from one another by the median foramen into the cavum internasale, which is represented as a distinct rounded protrusion in some specimens (e.g. PIUB Ro 4244b, Ro 4245b, MB Am.928.1–2). The posterior margin of the vomer can be traced in PIUB Ro 4245a but it is not clear whether it was separated from the palatine or whether the border between them is an artefact. The vomers and the lamina horizontalis of the maxillae border the fenestra exochoanalis anteriorly and anterolaterally. Each palatine bears a row of teeth on its lateral margin which diverge slightly posteriorly. The parasphenoid is widely rounded posteriorly but narrow anteriorly; however, outlines of this anterior region are obscured by the palatines.

Other cranial elements can be seen in some specimens preserved in ventral aspect. One is a distinct triangular elongated element located within the quadrate region of the holotype (Text-fig. 1); as the skeleton was dorso-ventrally compressed it could be interpreted either as the squamosal or, if it was displaced laterally, the pterygoid. Distinct imprints bordering the medial margin of the orbit and bifurcating anteriorly (tentatively interpreted as the lateral margin of the palatine in Text-fig. 2) are difficult to interpret but occur also in other specimens (Text-fig. 3B, marked by a single line). It is probable that the bifurcation delimits the fenestra endochoanalis (marked as 'choana' in Text-fig. 6A).

In dorsal view the quality of preservation of the skull prevents much information being obtained. PIUB Ro 4245a (Text-fig. 3A) shows fused facial processes of the premaxillae and, immediately posterior to them, a pair

of imprints that may represent parallel medial ridges of the nasals. Further posteriorly, the median suture may be traced, but the lateral margins of frontals and parietals are not distinct; however, in no specimen was the frontotemporal bridge found and apparently it was not developed. The maxilla does not reach posteriorly the level of the jaw articulation (Text-fig. 3A).

The hyobranchial apparatus consists of the copula anterior (= basihyal) which was articulated with the first ceratobranchials in some specimens (Text-figs 1, 4A), while in other specimens these structures seem to be confluent (Text-fig. 2). These differences may be explained in terms of variation in degree of ontogenetic development (only in fully developed individuals are both structures separated as in *Triturus*). In PIUB Ro 4245*b* (Text-fig. 3B) and probably (but not certainly) in MB Am.928.1–2 (Text-fig. 6A) similar elements are directed at their posterior ends towards the lower jaw, though anteriorly they are in contact with a median element that corresponds to the anterior copula. These elements thus can be interpreted, because of their different position, as the ceratohyals and not the first ceratobranchials. The absence of the ceratobranchials in PIUB Ro 4243 may be explained either by the loss of that part of the hyobranchial skeleton before fossilization or by insufficient ossification. The posterior tips of the ceratohyals were articulated with the epihyals (PIUB Ro 4245*b*; Text-fig. 3B). In other specimens, one (Text-figs 1, 4A) or several (Text-figs 2, 5–6) epibranchials may also be preserved. Although the articulated ossified branchial elements in most specimens recall the condition in normally developed *Triturus*, well-developed epibranchials are the principal evidence that *Brachycormus* was neotenous.

The vertebrae are opisthocoelous. The vertebral column consists of 12 (or 13) presacral vertebrae. Their spinal processes are dilated antero-posteriorly and their thickened (or even bifurcated, as suggested by BMNH 30268; Text-fig. 5) posterior part is somewhat protruding. Except for the atlas, the presacrals bear bicipital ribs. The rib associated with V3 bears a dorsal process, posteriorly situated in the flattened specimens, which is equal in length to the distance from its base to the tip of the rib (so the rib seems to be bifurcated distally as well; see Text-fig. 3). The rib of V4 has this dorsal spine shifted proximally. The remaining ribs do not have such processes. The caudal vertebrae are usually exposed laterally, because their tall neural spines and deep haemal processes (except for those on the first two caudals) resulted in the tail being twisted through 90° along the longitudinal axis and embedded in matrix in the horizontal position, as a result of post-mortem pressure. The posterior margin of both haemal and neural processes of the caudal vertebrae are thickened (Text-fig. 5) but this thickening cannot be recognized in some other specimens (Text-fig. 4B–C). The laminae on the haemal processes are not developed in the posterior caudal vertebrae (Text-fig. 5) whereas they are clearly visible on the neural processes. BMNH 30268 demonstrates the complete series of 34 caudal vertebrae.

From the elements of the shoulder girdle only the triangular scapula can be recognized (Text-fig. 3A). The ratio between the humerus and ulna (and also between the femur and tibia) deserves some attention (Table 1).

TABLE 1. Morphometric data of available material of *Brachycormus noachicus*. Abbreviations: LC, length of head; LtC, width of head; LH, length of humerus; LU, length of ulna; LF, length of femur; LT, length of tibia.

Specimen	Locality	LC:LtC	LH:LU	LF:LT
PIUB Ro 4429 (holotype)	Orsberg	1·13	1·78	2·1
PIUB Ro 4430	Orsberg	—	1·83	2·1
PIUB Ro 4053	Stösschen	—	1·56	—
PIUB Ro 4245	Orsberg	1·30	1·79	1·9
PIUB Ro 4244*b*	Orsberg	1·25	1·24	—
PIUB Ro 4244*a*	Orsberg	—	1·32	1·6
BMNH 30268	?Rott	—	1·61	2·06
MB MB.Am.928.1–2	?Orsberg	0·93	—	1·84
MB MB.Am.930.1	?Orsberg	0·95	1·87	—

LH:LU is 1·56–1·87 but in PIUB Ro 4244*a* and Ro 4244*b* (which represent two different individuals) the ratio is 1·24 and 1·32, respectively. These values suggest either rather wide intraspecific variation range or interspecific difference. The latter explanation seems to be supported by the fact that these differences are found

in individuals of the same size (hence supposedly of similar individual age) and from the same locality (Orsberg). However, these morphometric data cannot be supported by morphological ones because of poor state of preservation.

In the pelvic girdle, the pubis and ischium are usually preserved as ventral imprints, with characteristic outlines (Text-figs 1, 3). The carpus and tarsus were ossified. The carpus consists of three proximal elements, namely the radiale, intermedium and ulnare (Text-figs 1, 4A), and two elements located more distally (Text-figs 1–2); the carpal element surrounded by other bones may be interpreted as the centrale, the marginal carpal as the prepollex. The most distal row associated topographically with the metacarpals is of the distal carpals. Similarly, the tarsus consists of three proximal elements (fibulare, intermedium, tibiale; Text-fig. 4A); however, other tarsal elements are displaced so that it is difficult to determine them. The phalangeal formula is 2-2-3-3 in the manus and 2-3-4-?4-?2 in the pes.

Developmental status. The ossification of the carpus and tarsus, the ossification of most of the hyobranchial skeleton, and the presence of epiphyses on the long bones, all suggest that these animals were fully mature adults (except for PIUB Ro 4244*b*). It is difficult to deduce how much of the hyobranchial skeleton was also present in cartilaginous form, but the shape of the ossified components (the copula, both first ceratobranchials and both ceratohyals) suggests that it was similar to the condition occurring in the final stages of metamorphosis in the normal development of *Triturus*. The imprints of the posterior elements of the branchial arches (epibranchials) suggest that external gills were present. This may be taken as evidence that *Brachycormus* was neotenous.

Variation. Apart from characters which may depend on the state of preservation (proportions of skull, precise shape of bones), there is one obvious variable feature which may cast doubt on the view that all specimens belong to a single taxon. This is the shape of the haemal and neural processes of the caudal vertebrae. Whereas in PIUB Ro 4053 they are developed as thin, flat laminae, in BMNH 30268 these processes are clearly thickened along the posterior margins and in some vertebrae only these parts are preserved but not the laminae themselves (Text-fig. 5). Von Meyer (1860, p. 65) gave the total number of caudals as 36 or possibly more. This count is in approximate agreement with the condition in BMNH 30268 (Text-fig. 5), in PIUB Ro 4053 (von Meyer 1860, pl. 7, fig. 7 probably illustrated the skeleton in the original state when there was still a complete tail; however, the position of the distal section of the right fore extremity, which is different from that in Text-fig. 4B–C, may suggest that von Meyer also idealized his illustrations somewhat), and in a lost specimen (von Meyer 1860, pl. 7, fig. 8) which is the only known specimen of *Brachycormus* to be preserved in lateral aspect. This latter specimen has only spines instead of laminae with thickened posterior margins, as is the case with the posterior caudals in BMNH 30268. Moreover, the shape of the caudal vertebrae in PIUB Ro 4053 (Text-fig. 4B–C) is similar to that in the holotype of *Archaeotriton basalticus* (von Meyer, 1859), figured by von Meyer (1860, pl. 7, figs 9–10), but differs from it in the shape of the presacral ribs and smaller size so that it is clear that both are different taxa (see below). The same holds for another, poorly preserved specimen of *Archaeotriton* [NMP ČM 1421 (Pb 23)] from the Upper Oligocene of Varnsdorf described by Laube (1901). This has clearly expanded spinal processes, but is much larger than *Brachycormus*. It may be concluded that although the neural and haemal spines are similar in shape in taxa distinguishable on the basis of other characters (e.g. *Archaeotriton*), significant variation may occur in this character, perhaps dependent on the degree of ossification, as in living *Triturus*. For this reason, all the studied specimens are referred to a single taxon, despite their variation.

On the other hand, as suggested by the condition in contemporary species of *Triturus*, the main differences between the species should be expected in the structure of the skull. The postcranial skeleton is relatively uniform. Since the important diagnostic characters of the skull (e.g. the dorsal circumorbital region) are not sufficiently preserved, it remains possible that the known specimens of *Brachycormus noachicus* represent more than one species.

Geographical and stratigraphical occurrence. Until now, *Brachycormus* has been reported only from Orsberg, Stösschen and Rott in Siebengebirge, Germany, all of which are believed to be of uppermost Oligocene age (von Koenigswald *et al.* 1992, p. 313). The holotype of *Triturus opalinus* von Meyer, 1852 from Lužice (Lower

Miocene) in the Czech Republic, which may be conspecific with *Brachycormus* (see below for comparison), is based on a fragment of the postcranial skeleton and, consequently, important diagnostic characters are missing. However, it is not impossible that the specimen from Lužice (Text-fig. 9; see discussion below) represents a record of *Brachycormus* in another Central European locality.

THE ROLE OF NEOTENY IN THE TERTIARY CAUDATA

The presence of larval features in adult individuals with fully ossified skeletons is the simplest way to recognize neoteny in fossil urodeles. Neoteny (the shift of sexual maturity in premetamorphic stages) usually indicates deterioration of some aspect of the original normal environment. This may be either deterioration when aquatic habitats become surrounded by permanently harsh terrestrial conditions (Wilbur and Collins 1973), or deterioration when breeding seasons become shorter and periods of hibernation are prolonged due to increasing seasonality of climate. In the latter case, the animals are unable to complete their ontogenetic development over the normal time, i.e. the time which is usually available for complete development from egg to adult. However, the shift of appearance of some characters into earlier developmental stages is not necessarily accompanied by abbreviation of the chronological period in which morphogenesis of an individual is completed (i.e. is not accompanied by accelerated ontogenetic morphogenesis); quite the opposite – in amphibians it is usually associated with temporal prolongation of larval development. This clearly indicates that these animals are not able to complete their metamorphosis in time, due to unfavourable living conditions. In such cases, metamorphosis is postponed until conditions improve, provided that paedomorphosis is not genetically fixed.

The simplest example of a response to deterioration of climate manifested by prolongation of the cold seasons is an overwintering larva that hibernates and completes its metamorphosis in the following year. However, such developmental prolongation is associated with the retardation of sexual maturity, which is a disadvantageous phenomenon. Therefore, if long-term deterioration of climate causes such a situation to be repeated annually, then adaptations are developed that enable sexual maturity to be reached as in normal development. This seemingly results in a shift of sexual maturity into an earlier developmental stage (usually interpreted as acceleration of sexual development), but in fact it is the retardation of the somatic development; the sexual development is stable. When morphogenesis of the skeleton is retarded in this way, but the rate of ossification (which is dependent on time, not on morphogenetic degree attained) is normal, then the result is a neotenous individual, i.e. a permanent water dweller, with an ossified skeleton. This is no doubt the case with *Brachycormus*, as demonstrated by the hyobranchial skeleton and the expanded neural and haemal processes of the caudal vertebrae.

Timing of reproduction in paedomorphic and metamorphosed individuals of the same species is different, even under identical climatic conditions. For instance, paedomorphic adults of *Ambystoma talpoideum* lay eggs approximately six weeks earlier than terrestrial morphs, under the same living conditions. Early egg-laying and subsequent growth of hatchlings results in a significant size advantage for larvae from paedomorphic parents (Scott 1993). Also in *Triturus*, larval growth rate is higher and sexual maturity is attained sooner in paedomorphic forms (Kalezić *et al.* 1994). However, it should be noted that paedomorphosis may not only represent adaptation to deterioration of environmental conditions but may also occur for other reasons (see Whiteman 1994 and references therein for reviews).

When conditions become favourable in the long term, neotenous amphibians could be expected to invade dry land again and enter water only for breeding. It is obvious that such a shift in life strategy would be followed by the disappearance of gills and subsequent transformation of the hyobranchial apparatus into the hyoid. However, other features may remain unaffected and would retain their original paedomorphic state of somatic retardation. This might result in the retention of larval or juvenile characters which occurred in ancestral (neotenous) forms, even though living conditions correspond to those which existed before these ancestral forms were forced to adopt neoteny.

It is worth noting that neotenous features are usually associated with the viscerocranium because paedomorphs need to maintain branchial support of the gills. However, the branchial skeleton in *Brachycormus* is not preserved in the original larval form, but, judging from comparison with normal development in contemporary *Triturus alpestris* (Text-fig. 7), it corresponds to that of the
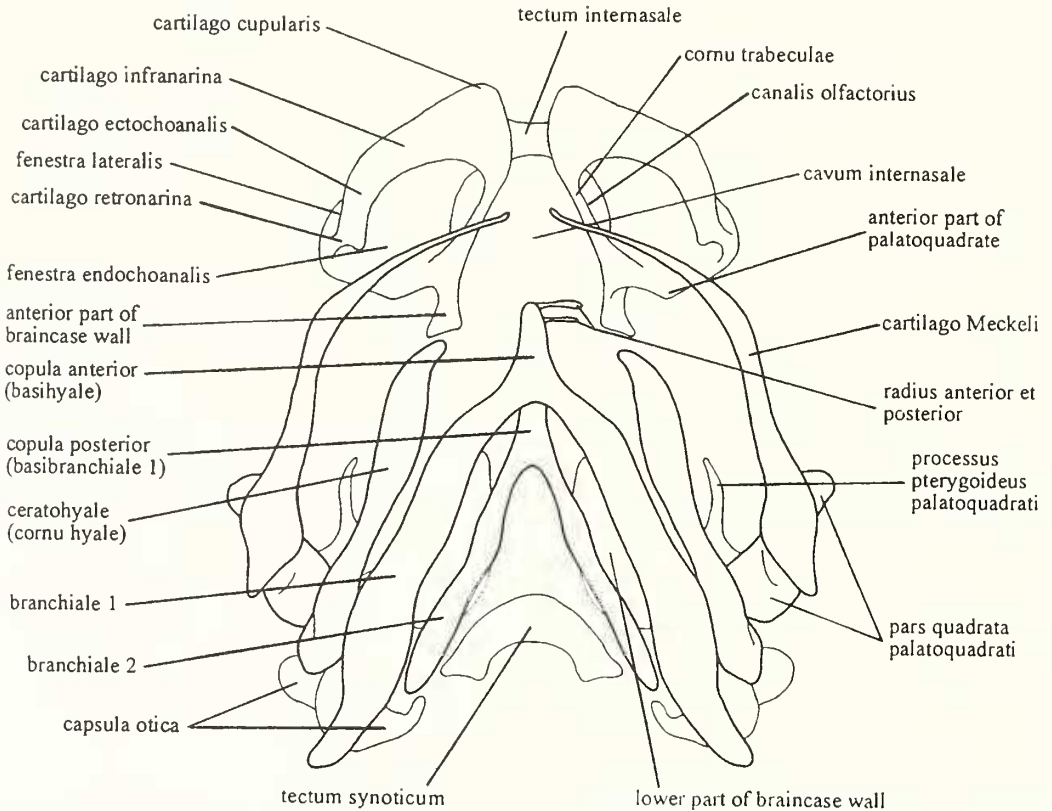
TEXT-FIG. 7. *Triturus alpestris* (Laurenti, 1768); neotenous individual from Drakolimni Greece; chondro-cranium in ventral view, reconstructed from serial sections.

final stages of metamorphosis. This means that restructuring developmental processes associated with metamorphosis (i.e. with the transition onto dry land) had already started but were blocked before their completion. As stated above, this can be caused either by prolongation of periods of inactivity (and corresponding shortening of breeding seasons) due to decrease of average temperature or, in contrast, by increase of average temperature and subsequent aridization making life on dry land difficult or impossible for insufficiently adapted forms. The former possibility may be illustrated by the irregular occurrence of overwintering larvae in central European populations of the Alpine newt [*Triturus alpestris* (Laurenti, 1768)] which is obviously correlated either with cold weather during the breeding season or the early onset of winter, or both. The second case may be exemplified by the occurrence of neotenous forms of *T. alpestris*, *T. vulgaris* and *T. carnifex* in the Balkan Peninsula (Roček 1974; Kalezić and Dzukić 1988; Kalezić *et al.* 1994). Aridization of climate in the Mediterranean area is a relatively recent phenomenon and this may explain why neoteny in these populations is only facultative and not genetically fixed. Both these contradictory reasons (decrease or increase of average temperatures) may have the same anatomical manifestations, namely retardation of developmental morphogenesis and shift of sexual maturity into earlier morphogenetic stages. This results in a larva capable of breeding.

In the Tertiary urodeles, the evolutionary step characterized as retarded developmental morphogenesis accompanied by a shift of sexual maturity was only subsequently followed by full ossification of the skeleton, including its branchial parts. In populations with facultative paedomorphosis, the metamorphic phenotype predominates in temporary ponds that dry out in most years, and the paedomorphic phenotype predominates in nearly permanent ponds (Semlitsch and Gibbons 1985; Semlitsch *et al.* 1990). Thus it seems that absence of a metamorphosed counterpart to the neotenous *Brachycormus* suggests the latter case and thus that the reason for neoteny in *Brachycormus* was not aridization of climate. This seems to be supported by the fact that the appearance of *Brachycormus*, as well as the neotenous forms of *Chelotriton*, is chronologically correlated with the Oligocene cooling event.

In general, the Oligocene was a period of significant cooling (Crowley and North 1991, p. 192) that started with a sharp drop in mean annual temperature in the early Oligocene and has continued to the present day, disregarding some temporary insignificant warm intervals. The Oligocene decline in mean annual temperature is estimated to have reached over 10 °C (Wolfe 1978, p. 699) and it was accompanied by a similarly profound shift in temperature equability so that the mean annual range of temperature which was 3–5 °C in the mid Eocene increased to 21–25 °C in the Oligocene (Wolfe 1978, p. 700; the data concern the Pacific Northwest of North America). A global mid Oligocene cooling event caused by glacio-eustatic fall in sea level has been proposed as the cause of selective extinctions of some vertebrate taxa (Prothero 1985). Moreover, in Europe the Oligocene (and Late Oligocene in particular) was a period of major geodynamic events that were no doubt reflected in climatic changes. In the Rupelian to Eochattian there was still a subtropical climate with a mean annual temperature of about 13–18 °C and non-seasonal rainfall in the area (shown by the palaeoflora of Witznitz, south of Leipzig; see Walther 1990, p. 154). The Late Oligocene palaeofloras of the same region, e.g. Borna, Bockwitz and Thierbach (Walther 1990, p. 155), however, indicate clear distinctions from the older complexes (appearance of arcto-tertiary elements), and suggest a comparatively cooler climate (annual mean temperature 4–13 °C) with longer winter seasons, which indicate clear deterioration of climate. The latter palaeofloras are, according to Walther (1990), similar to those found in Mainz Basin in the Vilbeler Schichten, and in Orsberg, Rott and Stösschen. Palaeoclimatic data obtained from analysis of palaeofloral changes in the molasse of western Switzerland (Berger 1990, p. 193) suggest that the relatively warm and humid climate of the Oligocene was terminated by a temperature and humidity crisis at the end of Oligocene, marked by disappearance of taxads and palms; this was followed by rising temperature but low humidity in the early Miocene. Cícha and Kováč (1990, p. 71) summarized climatic development in central Paratethys during the Egerian and concluded that, whereas the subtropical macro- and microflora are characteristic for the early and mid Egerian, a drop of temperature in the late Egerian is evidenced by appearance of deciduous arcto-tertiary elements. Later in the Miocene the climate improved again as shown by the presence of evergreen tree species.

This deterioration of climate (decrease in mean annual temperature and increase in mean annual range of temperature, i.e. increase in seasonality) meant that amphibians had to adapt to these new conditions, or withdraw from the region (the latter is the case, for instance, with *Andrias* and *Chelotriton* (*Tylototriton*) at the Plio–Pleistocene boundary). *Brachycormus*-like amphibians could obviously adapt themselves to a form of water-dwelling neotenous larva in order to compensate for deterioration of living conditions. Once favourable climatic conditions were restored again to allow metamorphosis, the normal adult stage could retain features which at the ancestral level were larval or juvenile (e.g. the incomplete frontotemporal bridge). This may be the case with *Triturus* which is readily derivable from *Brachycormus*, provided that the hyobranchial apparatus is developed until its final stage.

PHYLOGENETIC RELATIONS AND SYSTEMATIC POSITION

Brachycormus noachicus is similar to the common Tertiary species *Chelotriton paradoxus* in all characteristic features of the postcranial skeleton, such as opisthocoelous vertebrae with antero-
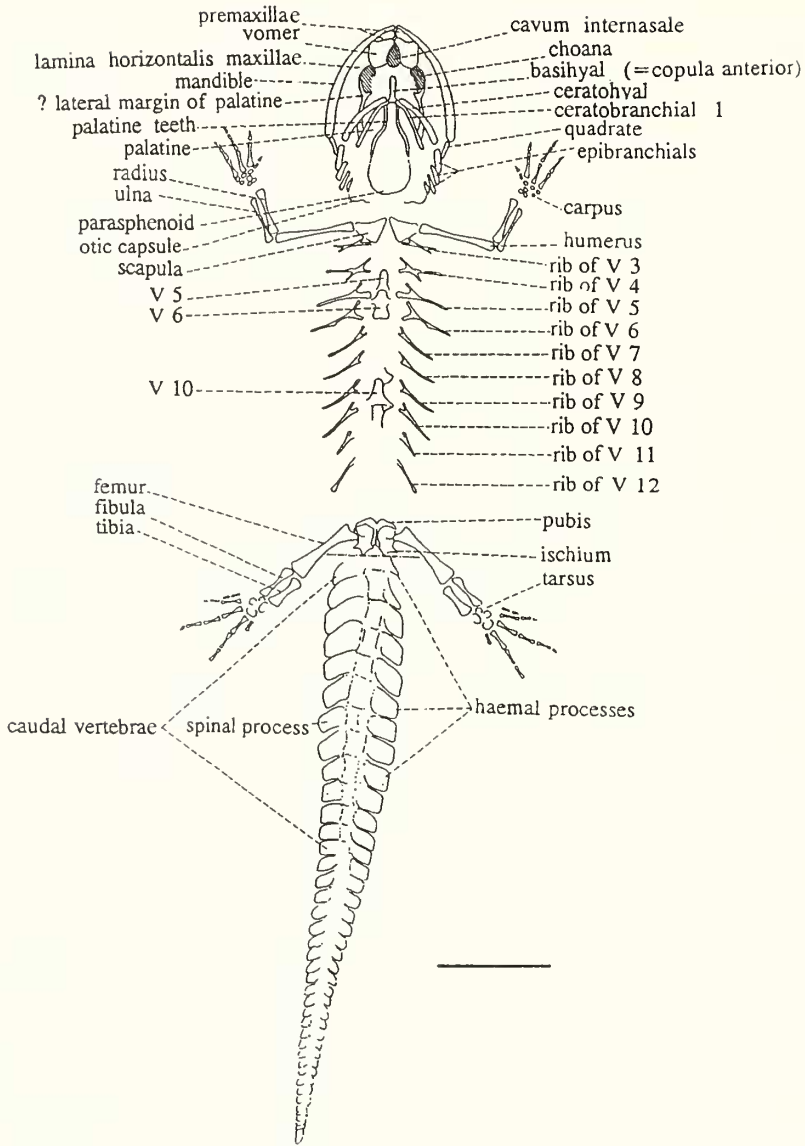
TEXT-FIG. 8. *Brachycormus noachicus* (Goldfuss, 1831). Reconstruction of skeleton in ventral view. The tail posterior to the transverse line is twisted through 90° along its longitudinal axis which corresponds to the preservational position. Scale bar represents 5 mm.

posteriorly expanded spinal processes, similarly enlarged haemal processes on caudals, bicipital ribs with dorsal spines, and the shape of the pelvis (Text-fig. 8). Also the basic structural scheme of the skull is similar (including the presence of an ossified hyobranchial skeleton). The principal difference is that *Chelotriton* is more heavily ossified. This is manifested both in the skull (all exocranial bones are large and covered with sculpture, often fused with each other, the frontotemporal arch is well-developed, the maxillary arch is complete, and at least some exocranial bones coalesced with endocranial ones) and in the postcranial skeleton (the spinal processes of most presacral vertebrae are terminated dorsally by a horizontal plate covered with sculpture which is similar to that on the

dermal bones of the skull). The reduced degree of ossification in *Brachycormus* may be explained by retarded osteogenesis in the lineage which split from the *Chelotriton* stock in the late Oligocene. However, neoteny had already appeared in the *Chelotriton–Brachycormus* lineage as demonstrated by the presence of the ossified hyobranchial apparatus in *Chelotriton paradoxus* (the earliest records of which are also from the Oligocene), but in a specimen of *Chelotriton robustus* from the Middle Eocene (Westphal 1980), it is absent. The same may hold for *Chelotriton* recorded from the Upper Eocene of England (Milner *et al.* 1982) but represented only by isolated vertebrae and few skull fragments. It may be supposed that the shift to neoteny was the first response to the Oligocene cooling, and retarded osteogenesis followed later.

It is obvious from the list of diagnostic characters given above that the difference between *Brachycormus* and *Triturus* is based primarily on the neoteny of the former. Hence, the question arises whether *Brachycormus* can be distinguished from *Triturus* as a separate genus only on the basis of neotenous features, or if it was only a neotenous lineage from within the *Triturus* radiation. At the present state of knowledge, this question is rather difficult to answer. The differences between the two taxa are situated only in the ventral part of the skull but not in the postcranial skeleton, and only in some details of the dorsal part of skull (e.g. frontotemporal bridge that may be developed to a variable degree in *Triturus* and presence of sculpture in its larger and better ossified species). The problem arises from the fact that all the material described as *Triturus* consists either of isolated vertebrae or of articulated postcranial skeletons; if the skull is present, the distinguishing characters are not observable or preserved. Until now, no *Triturus* skeleton has been found that clearly displays the ventral part of the skull. For all these reasons, and also because the hyobranchial apparatus in *Brachycormus* was ossified, whereas in Recent populations of *Triturus* where facultative neoteny occurs (which is, e.g., the case with the Greek populations of *Triturus alpestris*; see Text-fig. 7) it remains cartilaginous, one should maintain *Brachycormus* and *Triturus* as separate genera. Then, it is a matter of discussion whether neoteny is sufficient to distinguish these two taxa at generic or only specific level.

Brachycormus may also be compared with some other similar forms, regardless of uncertainty concerning their taxonomic validity. It is similar in size to the holotype of *Triturus opalinus*, from the Miocene locality of Lužice near Bílina (Czech Republic), which was preserved only as a set of posterior limbs (von Meyer 1852*a*, table 10, fig. 9) with ossified tarsus and with poorly preserved caudals. However, late in the nineteenth century, this specimen, originally deposited in the Lobkowitz collections in Bílina, was moved to Budapest where it was destroyed in 1956, so that direct comparison with *Brachycormus* is no longer possible. Estes (1981, p. 88) located another, nearly complete skeleton from Lužice in the collections of the National Museum, Prague [ČM 1462 (Pb 26, 27)]. This specimen is poorly preserved (Text-fig. 9) and the principal diagnostic structures, such as the ribs and distal parts of the limbs, are lacking. However, the size of animal, the shape of the caudal opisthocoelous vertebrae, and the fact that all preserved skeletal parts are fully ossified, recall *Brachycormus*. On the other hand, absence of some important elements in an otherwise articulated skeleton might support Estes's view that the individual was not fully grown.

Brachycormus resembles *Archaeotriton basalticus* (von Meyer, 1859) from the Upper Oligocene locality of Varnsdorf near Rumburk in north Bohemia (Czech Republic), in the presence of
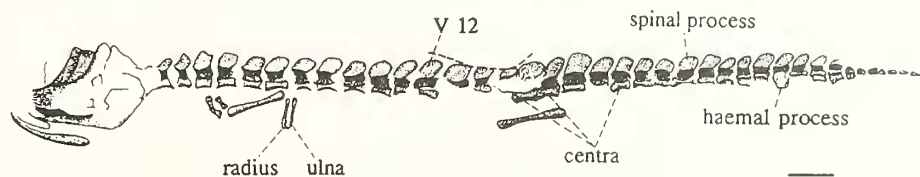
TEXT-FIG. 9. NMP ČM 1462 (Pb 26, 27). Miocene; Lužice near Bílina (north Bohemia, Czech Republic). Skeleton in lateral aspect, preserved in silicified diatomites. Scale bar represents 2 mm.
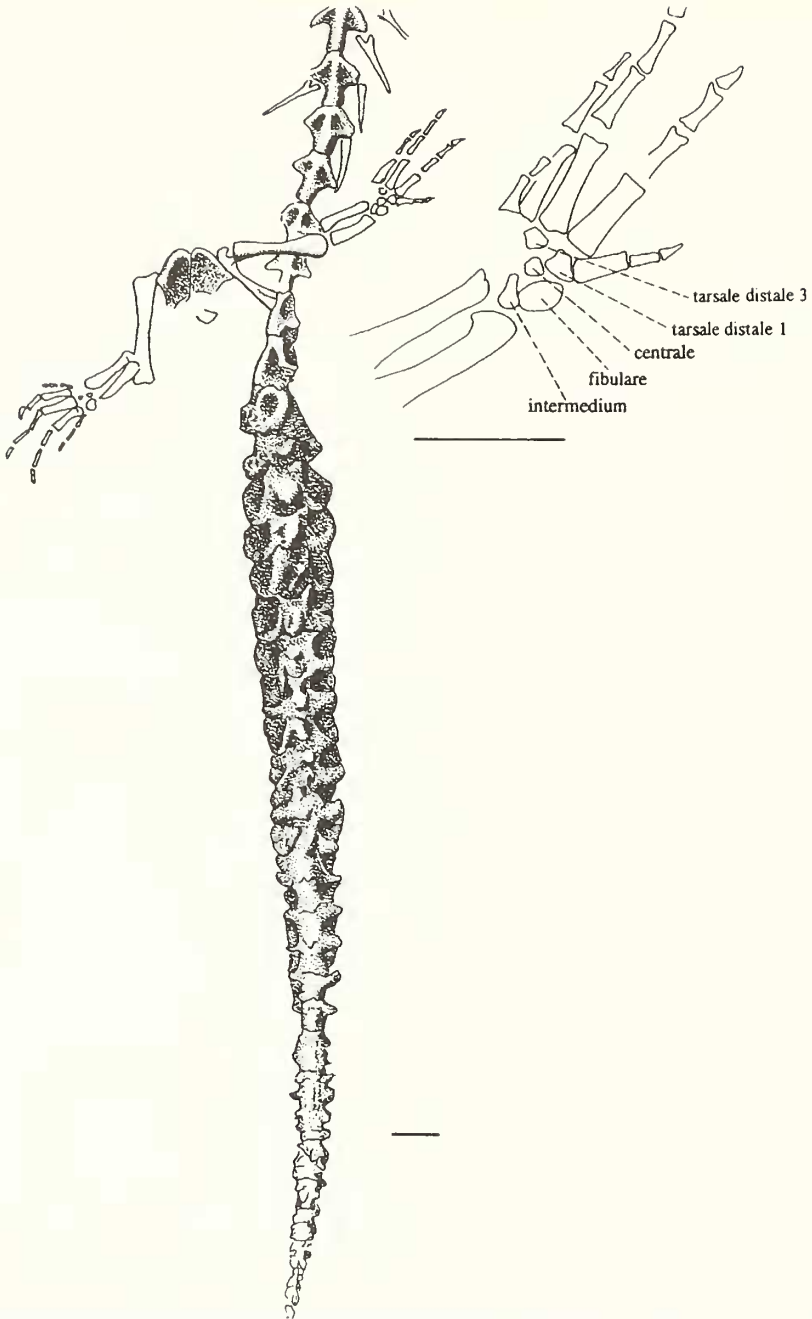
TEXT-FIG. 10. SMNS 58653. Part of postcranial skeleton of *Triturus*-like salamandrid from the Miocene of Randecker Maar (Germany). Presacral skeleton in ventral view, tail twisted through 90° along its longitudinal axis, preserving the lateral aspect along the horizontal plane of matrix. Scale bars each represent 2 mm.

opisthocoelous centra, the shape of the neural and haemal processes of the caudal vertebrae, the number of caudals (35), and in the ossified tarsal elements. However, according to von Meyer (1860, p. 72), who studied the holotype of *Archaeotriton*, the latter is twice as large as *Brachycormus* (its

size is similar to that of *Triturus cristatus*) and even the posterior presacral ribs bore distinct dorsal process. On the other hand, it agrees with *Brachycormus* in stratigraphical occurrence because it comes from a locality which is of Upper Oligocene age (see Špinar 1972, p. 22).

Judging from the opisthocoelous vertebrae, the shape of the ribs and pelvic elements, and similarities between *Brachycormus* and metamorphosing *Triturus* in the shape of the branchial skeleton and, to a lesser extent, other cranial features, these genera are closely related. Furthermore, *Triturus* and *Brachycormus* are similar in that the premaxillae are fused, the row of palatine teeth is straight or only moderately arch-like (not S-shaped), the posterior part of the parasphenoid is broad and oval, the posterior tips of the maxillae reach almost to the level of the quadrate, and the nasal process of the premaxillae is long and slender. On the other hand, *Triturus* differs from *Brachycormus* in having more developed exocranial bones (the *Triturus* species have the frontotemporal arch developed to various degree, starting from only signs of it in *T. alpestris* to complete connection in *T. helveticus*) (see also Haller-Probst and Schleich 1994). Larger and better ossified forms of *Triturus* (*T. cristatus*, *T. marmoratus*) bear even sculpture on some roofing bones. If it is theorized that the hyobranchial apparatus of *Brachycormus* continued to develop until its definite shape, then the stage found in *Triturus* would be achieved.

Occurrence of the underdeveloped frontotemporal arch in *Triturus* and its presence in contemporary *Pleurodeles*, *Tylototriton*, *Echinotriton* and in Oligo-Miocene *Chelotriton* suggest that all these genera are related. This view is supported also by the dorsal spines on the ribs (although variably developed), and by the dilated processes on the caudal vertebrae. Since *Brachycormus* is closely related to *Triturus*, as shown above, this form should be included into this group of salamandrid amphibians too.

Brachycormus and/or *Triturus*-like forms were probably widespread from the Oligocene through Pliocene of Europe. This is supported by SMNS 58653, the nearly complete posterior part of a postcranial skeleton (Text-fig. 10) from the Miocene of Randecker Maar (south Germany), which can be recognized as a similar form by the shape of the caudal vertebrae (twisted through 90° along its longitudinal axis), the shape of pelvis in dorsal view, the proportions of the hind limb, and the ossified tarsus. In all these characters, SMNS 58653 agrees with *Brachycormus*, but as the principal diagnostic characters of that genus are in the anterior part of the skeleton, it cannot be determined whether SMNS 58653 belongs to *Brachycormus* or to *Triturus*.

This example of *Brachycormus–Triturus* relationships (similar to the relations between *Chelotriton*, *Tylototriton*, *Echinotriton* and *Pleurodeles*) illustrates that recognition of phylogenetic relations between taxa represented by normal adult forms and those that are represented by neotenous individuals, or which passed through a neotenous stage in their history, is rather complicated and depends on a correct understanding of past evolutionary processes. If these relations are deduced only from character comparisons, then it is necessary to follow two approaches: (1) comparisons should be based on only those characters in neotenous or post-neotenous forms that occur both in larva and adult (i.e. strictly larval characters should be excluded); (2) if neotenous or paedomorphic characters are used in such analyses, then they must be compared with those in corresponding developmental stage of normal development (i.e. adult characters must be excluded). This seemingly obvious rule is often overlooked and all available characters are compared without evaluation of their evolutionary history.

paedomorphosis in the evolution of the Amphibia: evidence from paleontological and embryological data' supported by the Grant Agency of the Czech Republic (Grant No. 204/94/3001).

REFERENCES

BERGER, J.-P. 1990. Floral changes in the molasse of western Switzerland (Oligo-Miocene). Paleoclimatic implications. 189–194. *In* KNOBLOCH, E. and KVAČEK, Z. (eds). *Paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*. Geological Survey Publications, Prague, 323 pp.

BOLT, J. R. 1969. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science*, **166**, 888–891.

—— 1977. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. *Journal of Paleontology*, **51**, 235–249

—— 1979. *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications. 529–563. *In* NITECKI, M. H. (ed.). *Mazon Creek fossils*. Academic Press, London and New York, 581 pp.

CÍCHA, I. and KOVÁČ, M. 1990. Neogene climatic changes and geodynamics of the Central Paratethys. 70–78. *In* MINAŘÍKOVA, D. and LOBITZER, H. (eds). *Thirty years of geological cooperation between Austria and Czechoslovakia*. Federal Geological Survey, Vienna and Geological Survey, Prague, 288 pp.

CROWLEY, T. J. and NORTH, G. R. 1991. *Palaeoclimatology*. Oxford University Press and Clarendon Press, Oxford, 339 pp.

DECHEN, H. 1852. Geognostische Beschreibung des Siebengebirges. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westphalens*, **9**, 289–567.

ESTES, R. 1981. *Handbuch der Paläoherpetologie. Gymnophiona, Caudata*. Gustav Fischer Verlag, Stuttgart and New York, i–xv + 115 pp.

GOLDFUSS, A. 1831. Beiträge zur Kenntniss verschiedener Reptilien der Vorwelt. 2. Reptilien aus der schiefrigen Braunkohle. *Nova Acta Physico-Medica Academiae Cesareae Leopoldino-Carolinae Akademie der Natur-forscher*, **15**, 117–128.

GOULD, S. J. 1977. *Ontogeny and phylogeny*. Belknap Press of Harvard University Press, Cambridge, Massachusetts and London, England, i–ix + 501 pp.

GRAY, J. E. 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. *The Annals of Philosophy, New Series*, **10**, 193–217.

HALLER-PROBST, M. and SCHLEICH, H. H. 1994. Vergleichende osteologische Untersuchungen an einigen Urodelen Eurasiens (Amphibia: Urodela, Salamandridae, Proteidae). *Courier Forschungsinstitut Senckenberg*, **173**, 23–77.

HERRE, W. 1935. Die Schwanzlurche des mitteleocänen (oberlutetischen) Braunkohle des Geiseltales und die Phylogenie der Urodelen unter Einschluss der fossilen Formen. *Zoologica*, **87**, 1–85.

—— 1949. Neue Tatsachen zur Stammgeschichte der Schwanzlurche. *Zoologische Jahrbücher, Abteilung für Systematik*, **78**, 217–236.

—— 1955. Die Fauna der miozänen Spaltenfüllung von Neudorf a. d. March (CSR). Amphibia (Urodela). Fossile Urodelen aus dem Miozän des Wiener Beckens und ihre stammesgeschichtliche Bedeutung. *Sitzungsberichte der österreichischen Akademie des Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Abteilung A*, **164**, 783–803.

KALEZIĆ, M. L., CVETKOVIĆ, D., DJOROVIĆ, A. and DJUKIĆ, G. 1994. Paedomorphosis and differences in life-history traits of two neighbouring crested newt (*Triturus carnifex*) populations. *Herpetological Journal*, **4**, 151–158.

—— and DJUKIĆ, G. 1988. The frequent occurrence of paedomorphosis in the Smooth Newt (*Triturus vulgaris*) population from submediterranean area of Yugoslavia. *Amphibia–Reptilia*, **7**, 86–89.

KOENIGSWALD, W. VON, MARTIN, T., MÖRS, T. and PFRETZSCHNER, H. U. 1992. Die oberoligozäne Wirbeltierfauna von Rott bei Hennef am Siebengebirge. Synonymien und Literatur 1828–1991. *Decheniana (Bonn)*, **145**, 312–340.

LAUBE, G. C. 1901. Synopsis der Wirbelthierfauna der Böhm. Braunkohlenformation. *Abhandlungen des naturwissenschaftlichen-medizinischen Vereins "Lotos"*, **2**, 1–80.

LAURENTI, J. N. 1768. *Specimen medicum, exhiben Synopsin Reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum*. Trattner, Vienna, 214 pp., 5 tabs.

LYDEKKER, R. 1890. *Catalogue of the fossil Reptilia and Amphibia in the British Museum. IV. Anomodontia, Ecaudata and Labyrinthodontia*. British Museum, London, 295 pp.

MEYER, H. VON 1852a. Die tertiären Süsswassergebilde des nördlichen Böhmens und ihre fossilem Thierreste. III. Beschreibung der fossilen Decapoden, Fische, Batrachier und Säugethiere aus den tertiären Süsswassergebilden des nördlichen Böhmens. *Palaeontographica*, **2**, 43–73.

—— 1852b. Mittheilungen an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde*, **1852**, 465–468.

—— 1858. Mittheilungen an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde*, **1858**, 202–207.

—— 1859. Mittheilungen an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde*, **1859**, 723–725.

—— 1860. Salamandrinen aus der Braunkohle am Rhein und in Böhmen. *Palaeontographica*, **7**, 43–73.

—— 1863. *Heliarchon furcillatus*, ein Batrachier aus der Braunkohle von Rott im Siebengebirge. *Palaeontographica*, **10**, 292–298.

MILNER, A. C., MILNER, A. R. and ESTES, R. 1980. Amphibians and squamates from the Upper Eocene of Hordle Cliff, Hampshire, – a preliminary report. *Tertiary Research*, **4**, 149–154.

MILNER, A. R. 1988. The relationships and origin of living amphibians. 59–102. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods. Vol. 1: Amphibians, reptiles, birds*. Systematics Association Special Volume 35A. Clarendon Press, Oxford, 377 pp.

PROTHERO, D. R. 1985. Mid-Oligocene extinction event in North American land mammals. *Science*, **229**, 550–551.

ROČEK, Z. 1974. Beitrag zur Erkennung der Neotenie des Alpenmolches *Triturus alpestris* (Laurenti, 1768). *Věstník Československé Společnosti Zoologické*, **38**, 285–294.

SCOPOLI, I. 1777. *Introductio ad historiam naturalem sistens genera lepidum, plantarum, et animalium*. Wolfgang Gerle, Prague, 506 + xxxiv pp.

SCOTT, D. E. 1993. Timing of reproduction of paedomorphic and metamorphic *Ambystoma talpoideum*. *American Midland Naturalist*, **129**, 397–402.

SEMLITSCH, R. D. and GIBBONS, J. W. 1985. Phenotypic variation in metamorphosis and paedomorphosis in the salamander *Ambystoma talpoideum*. *Ecology*, **66**, 1123–1130.

—— HARRIS, R. N. and WILBUR, H. M. 1990. Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. *Evolution*, **44**, 1604–1613.

ŠPINAR, Z. V. 1972. *Tertiary frogs from Central Europe*. Academia, Prague, 286 pp.

WALTHER, H. 1990. The Weisselster Basin (GDR) – an example of the development and history of Paleogene forest vegetation in Central Europe. 149–158. *In* KNOBLOCH, E. and KVAČEK, Z. (eds). *Paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*. Geological Survey Publications, Prague, 256 pp.

WARREN, A. A. and HUTCHINSON, M. N. 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaurid skull. *Palaeontology*, **31**, 857–876.

——–—— 1990. *Lapillopsis*, a new genus of temnospondyl amphibians from the Early Triassic of Queensland. *Alcheringa*, **14**, 149–158.

—— and SCHROEDER, N. 1995. Changes in the capitosaur skull with growth: an extension of the growth series of *Parotosuchus aliciae* (Amphibia, Temnospondyli) with comments on the otic area of capitosaurs. *Alcheringa*, **19**, 41–46.

WESTPHAL, F. 1980. *Chelotriton robustus* n.sp., ein Salamandride aus dem Eozän der Grube Messel bei Darmstadt. *Senckenbergiana lethaea*, **60**, 475–487.

WHITEMAN, H. H. 1994. Evolution of facultative paedomorphosis in salamanders. *The Quarterly Review of Biology*, **69**, 205–221.

WILBUR, H. M. and COLLINS, J. P. 1973. Ecological aspects of amphibian metamorphosis. *Science*, **182**, 1305–1314.

WOLFE, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist*, **66**, 694–703.

ZBYNĚK ROČEK

Department of Paleontology
Geological Institute, Academy of Sciences
Rozvojová 135, CZ-165 00 Prague 6
Czech Republic